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Sutochnye vertikal'nye migratsii nekotorykh rakoobraznykh
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61*

Daily vertical migrations of some crustaceans
in the Baltic Sea

I. I. Nikolaev

VERTICAL MIGRATIONS OF MYSIDS

It has been known for a long time that mysids in the
Baltic Sea display daily vertical migrations. Apstein wrote
about this as long ago as 1905, and subsequently this phenom-
enon was mentioned in studies by other authors (2, 5, 6, 7,
8, 9, 10). The mysid species which are present in massive
numbers in the Baltic accomplish clearly expressed daily ver-
tical migrations, with a span of 100 m and more. These may

* The numbers in the right-hand margin indicate the corres-
ponding pages in the original text. (Tr.).

serve as a good illustration of the protective-adaptive characteristics of aquatic organisms (5).

In studying the migrations of mysids we were able to obtain more precise information on some quantitative characteristics of this phenomenon, namely: the times of the diurnal (benthopelagic) and nocturnal (pelagic) phases of distribution in different seasons, as well as the rate and span of the vertical migrations.

1. Duration of the benthopelagic and pelagic phases of distribution of mysids. The vertical migrations of Mysis mixta were studied in July in the central part of the sea (southern part of the Gotland basin) and in June and August in the Gulf of Riga¹. The mysids were caught with an ichthyoplanktonic net, having an 80 cm entry opening diameter, or with a 37 cm diameter Juday net. The gradation (step intervals) of the vertical series in the Baltic comprised 10 m, while in the Gulf of Riga this ranged from 10 to 2 m. The series were taken every 2-4 hours during the periods of the steady diurnal and nocturnal regimes, and every 15-20 minutes during the transitional periods (morning and evening twilight). The detailed studies of the migrations were carried out in all cases with an illumination intensity approximating to the normal intensity for the corresponding period.

The results of the studies of the vertical series are presented in Tables 1-3. In Table 1 are presented the results of the vertical distribution of Mysis mixta on the 13th and 14th of July 1955 in the region of Klaipeda. From the data in the

¹ Valuable studies on the vertical migrations of mysids in the Gulf of Riga were carried out in the summer of 1956 by the students V. A. Godlevskaya and L. V. Sanina.

Table 1.

А. Горизонты лова в м	Таблица 1					
	В. Время наблюдения* в час. и мин.					
	21.30-22.00	22.00-22.30	0.30-1.00	1.30-2.00	2.30-3.00	3.30-4.00
С. количество экземпляров на 1 м ³						
0-10	0	0	0	0	0	0
10-20	0	0,5	5,5	1,5	0	0
20-50	0	3,0	7,0	10,0	0,3	0
50-60	1	1,0	1,0	5,0	17,0	0

* Часы во всех таблицах приводятся по местному времени.

A - Netting horizons in m

B - Times of observation* in hours and minutes

C - number of specimens per 1 m³

* The times in all the tables are given according to local time.

table it is evident that the benthopelagic (diurnal) phase of the distribution of Mysis mixta lasts about 20 hours (from 02.30 - 03.00 to 22.00 - 22.30), while the pelagic (nocturnal) phase of the distribution lasts about 4 hours (22.00 - 22.30 to 02.30 - 03.00). The time from 02.30 to 03.00 may be considered as transitional from the pelagic (nocturnal) phase of distribution to the benthopelagic (diurnal) phase of distribution, while the period between 22.00 and 22.30 is also transitional but now in the opposite direction.

The results of the studies of the June series (1955) in the Gulf of Riga are presented in Table 2, and of the August series (1957) - in Table 3.

A marked similarity is found in the duration and periods of the pelagic and benthopelagic phases of distribution with that which was noted in the open sea in July, and in the

Table 2

Таблица 2

A. Горизонты лова в м	B. Виды мизид	C. Часы наблюдений						
		16-18	18-20	20-22	22-23	24.00-2	2-4	4-6
		D. количество экземпляров на 1 м ³						
0-20	Mysis mixta	0	0	0,8	0,5	0,5	0	0
	Mysis oculata	0	0	7	2	1	0	0
20-40	Mysis mixta	0	0	0	0	0	0	0
	Mysis oculata	0	1	4	1	2	0,5	0

A - Netting horizons in m

B - Species of mysids

C - Times of observation

D - number of specimens per 1 m³

Table 3

Таблица 3

А. Горизонты лова в м	В. Время наблюдений в час. и мин.							
	20.00—20.30		20.50—21.18		23.40—00.05		3.00—3.15	
	С. количество экземпляров в 1 м³							
	M. mixta	M. oculata	M. mixta	M. oculata	M. mixta	M. oculata	M. mixta	M. oculata
0—10	0	0	0	0	0	0	0	0
10—15	0	0	0	2	0	2	0	2
15—20	0	0	0	4	2	0	0	0
20—25	0	0	4	2	2	0	0	0
25—30	0	0	2	2	4	2	0	0
30—35	0	0	0	2	2	0	4	0
35—40	8	0	0	0	0	0		

A - Netting horizons in m

B - Times of observation in hours and minutes

C - number of specimens in 1 m³

gulf this was followed not only for M. mixta but also for a second species that occurs in massive numbers, M. oculata v. relicta.

The benthopelagic (diurnal) phase of distribution in the Gulf of Riga commenced from 02.30 - 03.00, i.e. at the same

time as was the case in July in the Baltic, though it finished somewhat earlier than in the open sea, at 21.30 - 22.00. The conditions of the natural illumination in June and July may be accepted as being the same. For this reason the differences in the duration and periods of the pelagic and benthopelagic phases of distribution in the gulf and in the sea may be explained by differences in the transparency of the water or by other factors.

In August the duration of the phases of the pelagic and benthopelagic distribution changed markedly as compared to the June - July observations. In the Gulf of Riga (see Table 3) the ascent of the mysids into the upper horizons of the water lasted from 20.30 to 21.18, while the descent occurred from 03.20 to 03.45. Consequently, the mysids were found at this time in the middle layers of the water for about 6.5 hours, and in the benthopelagic layer (diurnal distribution) for 17.5 hours.

A large number of observations on the vertical migration of mysids were carried out in the autumn, when the migrations are manifested most clearly. The data from the autumn observations provide a picture of the times and periods of the benthopelagic and pelagic phases of the distribution of the mysids. The results of the study of a large number of autumn series (see Tables 4 - 6) allow us to conclude that the ascent of the mysids in the water layers occurs at 19.00 - 20.00 in September and at 18.00 - 19.00 in October; the descent occurs at 04.00 - 05.00 in September and at 05.00 - 06.00 in October.

The daily changes in the numbers of mysids in the plankton in the Gulf of Riga (September 30 - October 1, 1954) are

Table 4

Таблица 4

А Горизонты ловов в м	В Виды мизид	С Количество экземпляров в толще воды под 1 м ² при наблюдении в часы							
		14-16	16-18	18-20	20-21	21-22	23-24	8-10	10-12
0-10	Mysis mixta	0	0	0	10	20	0	0	0
	Mysis oculata	0	0	0	0	0	0	0	0
	Neomysis vulgaris . . .	0	0	0	190	10	0	0	0
10-20	Mysis mixta	0	0	0	10	0	40	0	0
	Mysis oculata	0	0	0	0	0	10	0	0
	Neomysis vulgaris . . .	0	0	0	130	0	0	0	0
20-30	Mysis mixta	0	0	0	60	40	30	50	0
	Mysis oculata	0	0	0	0	10	130	130	0
	Neomysis vulgaris . . .	0	0	140	70	0	0	20	0
30-40	Mysis mixta	0	100	—	—	0	—	20	0
	Mysis oculata	0	100	—	—	60	—	10	0
	Neomysis vulgaris . . .	0	130	—	—	0	—	0	0
D. Всего мизид в слое 0-40 м		0	330	140	470	140	210	230	0

A - Netting horizons in m

B - Species of mysids

C - Number of specimens in water column under 1 m²
with observations in hours

D - Total number of mysids in 0-40 m layer

presented in Table 4.

The daily changes in the numbers of mysids in the plankton in the Gulf of Riga at a depth of 43-39 m (20-24 September 1958) are given in Table 5.

The daily changes in the numbers of mysids in the plankton in the Gulf of Riga from 11-16 October 1950, according to data from six stations, are presented in Table 6.

In Table 7 are given the daily changes in the numbers of mysids in the plankton in the Gulf of Riga (Kolkas region) on 11-12 May 1954.

Table 5

Таблица 5

A Виды мизид	B Количество экземпляров в толще воды под 1 м ² при наблюдении в часы							
	18-20	20-22	22-24	24-2	2-4	4-6	8-9	12-14
<i>Mysis mixta</i>	0	92	144	156	80	80	44	0
<i>Mysis oculata</i>	0	324	180	660	268	184	164	0
<i>Neomysis vulgaris</i>	0	8	8	20	28	8	8	0
C Всего мизид	0	424	332	835	376	272	216	0

Table 6

Таблица 6

A Виды мизид	B Количество экземпляров в толще воды под 1 м ² при наблюдении в часы									
	14-16	16-18	18-20	22-24	24-2	2-4	4-6	6-8	8-10	10
<i>Mysis mixta</i>	0	4	42	76	52	120	66	56	71	0
<i>Mysis oculata</i>	0	2	22	144	60	12	36	11	1	0
<i>Neomysis vulgaris</i>	0	0	108	28	104	48	122	22	11	0
C Всего мизид	0	6	172	248	216	180	224	89	83	0

A - Species of mysids

B - Number of specimens in water column under 1 m²
with observations in hours

C - Total number of mysids

In summarizing the data from all of the vertical series, obtained from May to October, we may compile, in first approximation, a scheme of the annual changes in the times of transition of the mysids from the benthopelagic to the pelagic phase (ascent in evening twilight) and from the pelagic to the benthopelagic phase (descent in morning twilight), and,

Table 7

Таблица 7

А Горизонты лова в м	В Виды мизид	С Количество экземпляров в толще воды под 1 м ² при наблюдении в часы				
		22-23	24-1	4-5	11-12	22-23
0-10	<i>Mysis mixta</i>	0	0	0	0	0
	<i>Mysis oculata</i>	0	0	0	0	0
10-20	<i>Mysis mixta</i>	0	30	0	0	0
	<i>Mysis oculata</i>	0	30	0	0	0
20-30	<i>Mysis mixta</i>	20	380	60	0	30
	<i>Mysis oculata</i>	80	190	280	0	10
	<i>Neomysis vulgaris</i>	0	10	0	0	0
30-38	<i>Mysis mixta</i>	0	0	40	0	10
	<i>Mysis oculata</i>	0	0	100	0	20
D Всего мизид в слое 0-38 м . .		100	630	480	0	80

A - Netting horizons in m

B - Species of mysids

C - Number of specimens in water column under 1 m²
with observations in hours

D - Total number of mysids in 0-38 m layer

correspondingly, of the changes of these phases according to the months. The dynamics of the principal indices of the daily vertical migrations of *M. mixta* in the Gulf of Riga from May to January, with calm cloudless weather, are shown in Table 8.

The process of the vertical migration of the mysids, the duration and periods of the sojourn of the latter in the two basic phases of the vertical distribution are affected by several physical and biological factors. Under the influence of these factors the corresponding indices, coinciding with particular time periods, may be shifted. An especially large effect on these migrations (in the sense of the deviation from

Table 8

Таблица 8

Месяцы Months	А Часы миграций		D Продолжительность фаз в часах	
	б подъем	с погружение	е ночная (пела- гическая)	ф дневная (придонная)
Май . . . May	20-21	3-4	6-8	16-18
Июнь . . . June	21-22	2-3	4-6	18-20
Июль . . . July	21-22	2-3	4-6	18-20
Август . . . August	20-21	3-4	6-8	16-18
Сентябрь . . . September	19-20	4-5	8-10	14-16
Октябрь . . . October	18-19	5-6	10-12	12-14
Ноябрь . . . November	17-18	6-7	12-14	10-12
Декабрь . . . December	16-17	7-8	14-16	8-10
Январь . . . January	16-17	7-8	14-16	8-10

*Примечание. Данные за декабрь и январь интерполированы. Ошибка не превышает ± 4 минут.

A - Times of migration

b - ascent

c - descent

D - Duration of phases in hours

e - nocturnal (pelagic)

f - diurnal (benthopelagic)

* Note. Data for December and January interpolated. The error does not exceed ± 40 minutes.

the norm of their periods) is manifested by factors which directly or indirectly decrease the natural illumination: cloudiness, fog, precipitation, rough seas and ice cover. Of considerable significance among the biological factors is the age composition of the mysids (young forms, as a rule, swim up higher and remain longer in the pelagic phase than do the adult forms), as well as the intensity of feeding. However, we do not yet possess reliable quantitative indices of the influence of these factors on the migrations.

2. Rate of migration. The capacity of mysids to migrate vertically is of practical interest, since the transition of the mysids from the pelagic to the benthopelagic phase of distribution, and vice-versa, affects the rates of the vertical migrations of fishes that feed on these organisms. The studies have shown that the vertical migrations of mysids are accomplished in bursts, rather than smoothly, and the transition from one phase of the daily distribution into the other proceeds within a comparatively short period.

The data from vertical catches show that in June M. mixta migrated from the benthopelagic layer (61 m) to the 10-20 m horizon in 30 minutes, at an average speed of 80-100 m per hour, and in the reverse direction in 20-25 minutes, at a speed of up to 120 m per hour.

In the Gulf of Riga on August 14th the ascent of Mysis mixta from the benthopelagic layer (35-40 m) to the 10-15 m horizon proceeded during the period from 20.55 to 21.18, while the descent occurred between 03.20 and 03.45 (Figure 1).

Consequently, the ascent of mysids over a distance of up to 40-60 m from the bottom occurs within 40-50 minutes (in individual cases within 25-30 minutes), while the migration in the opposite direction occurs within 30-40 minutes. This refers to both M. mixta and to M. oculata var. relicta.

Thus, the rate of the vertical migrations of the Baltic mysids is very considerable - up to 1-1.4 m/minute (this pertains to the rate of migration of clusters of mysids; separate individuals obviously migrate even more rapidly, especially over a small distance).

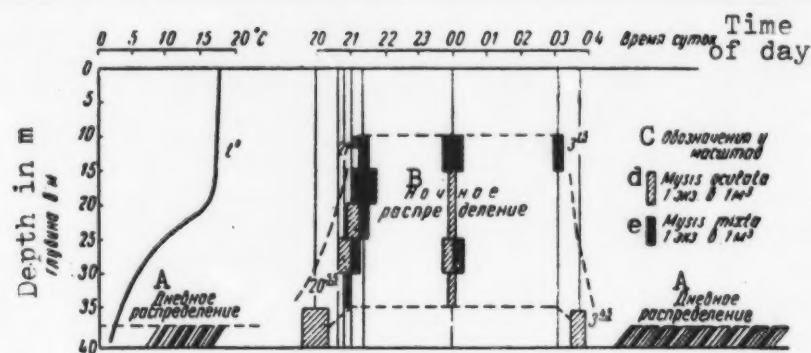


Рис. 1. Вертикальное распределение *Mysis mixta* и *Mysis oculata* var. *relicta* в Рижском заливе 14—15 августа 1957 г.

Figure 1. Vertical distribution of *Mysis mixta* and *Mysis oculata* var. *relicta* in the Gulf of Riga on August 14 - 15, 1957.

- A - Diurnal distribution
- B - Nocturnal distribution
- C - Legend and scale

- d - *Mysis oculata* 1 specimen in 1 m³
- e - *Mysis mixta* 1 specimen in 1 m³

Several authors have noted the high comparative (relative) rate of migration of invertebrates during their vertical migrations. Thus, according to Bogorov (1), *Eurytemora grimmeri* in the Caspian migrates at a rate of 15 cm a minute; *Calanus* in the region of San Diego migrates at a speed of not less than 20 - 30 cm a minute, while in the region of Plymouth it migrates at up to 10 cm a minute (3). According to the data of Hardy and Bainbridge (13), *Calanus finmarchicus* may display a migration rate of 66 m/hour upwards and 107 m/hour downwards over 2 minutes, and over a prolonged period of time - correspondingly, 15 and 47 m/hour. The euphausiid *Meganycetifanes* migrates at a rate of about 130 m/hour over an extended

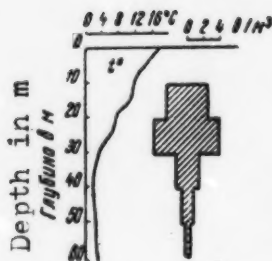


Рис. 2. Вертикальное распределение *Mysis mixta* в центральной Балтике (район Клайпеды) 14 июня 1955 г.

Figure 2.

Vertical distribution of *Mysis mixta* in the central Baltic (region of Klaipeda) 14 June 1955.

period of time, and at about 215 m/hour over a short period; the nauplii of *Calanus* migrate at a rate of 15 m/hour over an extended period, and at 23 m/hour over a brief period.

3. Distribution of mysids in the water mass during the night period. The overall zone of the distribution of mysids in the pelagic zone may comprise 60 - 80 m along the vertical, in some cases 100 - 120 m (and even 160 - 180 m), but the zone of greatest concentration (the "mysid zone") occupies not more than 10 - 15 m, and sometimes only 3 - 4 m. More rarely this zone may be poorly expressed, when the mysids are distributed comparatively evenly over a distance of 40 - 50 m.

In the summer (in June - July) in the Baltic the greatest concentrations of mysids are found at night in the layer from 20 to 50 m, most frequently in the 20 - 30 m layer, i.e. in the thermocline zone or slightly below this. In July 1955 in the open sea the maximal numbers of *M. mixta* were noted in the 20 - 30 m layer at a water temperature of from 7.7° (20 m) to 4.9° (30 m); fairly large numbers were also present in the 10 - 20 m layer at a temperature of from 12.2 to 7.7° (Figure 2).

The mysid zone was expressed very clearly on the 25th of October 1955 in the Kolkas region of the Gulf of Riga. The maximal concentration of mysids during the entire period of our studies on the Baltic (1946-1957) was recorded here: 2560 individuals under 1 m². The accumulation was made up of three species: Mysis mixta - 50.2%, M. oculata relicta - 45.6% and Neomysis - 4.2%. The main part was concentrated in the layer from 28 to 30 m (site depth 41 m), which was established not only by detailed netting of the water column with a plankton net but also by echo sounder records.

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According to the data from joint Soviet-Finnish oceanographic studies in 1956, large numbers of mysids were found in the Gulf of Bothnia in June 1956: in the middle of the night in the 0-50 m layer there were up to 894 M. oculata relicta and 298 M. mixta under 1 m². In the middle of the day (at 11.30) the largest accumulations of mysids were noted at a depth of from 80 to 100 m.

The two species of mysids which are most abundantly present in the open waters of the Baltic and of its large gulfs (Gulfs of Riga, Finland and Bothnia), M. mixta and M. oculata relicta, belong to the Baltic-Arctic relict complex. The representatives of this complex reproduce in the Baltic only during the winter or predominantly during the cold half of the year. On the basis of this ecologico-geographical characteristic of these mysid species one might expect that their nocturnal migrations from the benthopelagic layer up into the mass of the water during the summer, under conditions in the Baltic, should be restricted to the thermocline zone. In fact, however, this is not always the case. Even in the middle of

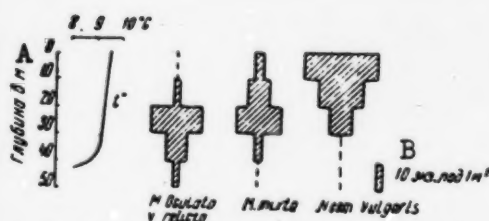


Рис. 3. Среднее вертикальное распределение основных видов мизид в Рижском заливе ночью в октябре 1954 г.

Figure 3. Average vertical distribution of the principal species of mysids in the Gulf of Riga at night in October 1954.

A - Depth in m

B - 10 specimens under 1 m²

the summer a small part of the population of both species swims up to a depth of 10-15 m, and at the beginning of the autumn - up to the surface of the water, where the temperature is 14-16°. Although the greatest concentration of these species during the summer and autumn is found at night in the thermocline zone, the migration of the mysids is nevertheless influenced not only by the temperature gradient but also by the concentration of the plankton on which the mysids feed.

More detailed observations show that the migration ranges and the location of the zone of greatest concentration differ in the different species of mysids. Of the three principal species, the inshore thermophilic species Neomysis vulgaris ascends to the highest level at night and forms the highest tier of the nocturnal accumulation (mysid zone), while the most cold-water species M. oculata ascends to the lowest level. These differences are clearly displayed in the Gulf of Riga in the autumn, when all three species are encountered here in large numbers. Thus, for example, in September - October 1954

at night the maximal numbers of Neomysis were present in the 10-0 m layer; the maximal numbers of the two species of Mysis were found in the 20-30 m layer, though M. oculata was scarcely encountered at all above this layer, while, conversely, M. mixta was scarcely encountered below 30 m and 38% of its population was found above 20 m. The vertical distribution of these species at night from September 25 to October 5 in 1954 (average data) are illustrated in Figure 3.

During the day the mysids distribute themselves above the bottom, where they also form a certain zone of accumulation. In the summer in the middle of the day at depths of up to 50-60 m, in the central part of the sea, M. mixta remains in the benthopelagic layer. In these conditions a Sigsby trawl, which nets out the layer from 0 to 0.5 m from the bottom, brings in the most mysids. This applies to depths of up to 70-80 m in the open sea and up to 30-40 m in the Gulf of Riga. At depths of 80-100 m the mysids no longer adhere so closely to the bottom during the day, and with a further increase in the depth the zones of their diurnal accumulation become distributed farther and farther away from the bottom. In the Gulf of Riga at depths of 40-50 m (in the central basin zone) Mysis mixta and Mysis oculata do not move away more than 2-3 m from the bottom during the day in sunny weather.

At the present time we do not yet have sufficient data to indicate precisely that depth, commencing from which the mysids (M. mixta and M. oculata) in the Baltic do not descend to the bottom during the day. Judging by the fact that at depths of 120-140 m a trawl net moving at a height of about 3 m from the bottom still brings in a considerable number of

mysids, while at depths of 150-180 m they are even taken in a plankton net in the lower layer, it may be assumed that at depths of 120-150 m the zone of mysid accumulation during the day extends to 2-3 m from the bottom, while at depths of 150-180 m this zone extends to 30 m from the bottom.

VERTICAL MIGRATIONS OF AMPHIPODS

Of this species complex Pontoporeia affinis and P. femorata perform distinct vertical migrations. During the course of the entire year both of these species are caught in both benthic (bottom drags, dredges) as well as pelagic (plankton nets) fishing gear, though in the latter they are caught only at night.

The amplitude of the migrations of these crustaceans is sometimes as great as 100-150 m. For example, in the Gulf of Bothnia in June 1956 at a depth of 195m two specimens of P. affinis were caught with a Genzen* net in the 100-0 m layer. Hessle and Vallin (10) cite the fact of the capture of a specimen of P. affinis in the Landsort basin in the 50-0 m layer at a station depth of 200 m.

In the spring and summer a very minute part of the population of these species (not more than 1%) accomplishes large migrations (moving away from the bottom to a distance of several tens of meters); in the autumn, however, no less than 15-20% and possibly even 50% of the population migrate.

Thus, for example, in November 1956 in the Gulf of Riga, in the region of Rukhnu Island, 893 individuals were caught with a plankton net under 1 m². Although during the

* "set' Genzena" - could be a Gensen or Hensen net? (Tr.).

summer (from June to August) in this region in some years the density of accumulation of Pontoporeia on the bottom was as high as 7000 individual per 1 m², in November, however, we did not find more than 2000 individuals per 1 m² on account of the intensive feeding on this crustacean by fishes during the summer and autumn. In this case, judging by the fact that the main part of the migrating crustaceans were concentrated in the uppermost layer of the water, it may be assumed that up to 50% of the population of this species was found at night in the pelagic zone.

Below is presented the vertical distribution of P. affinis in the pelagic zone in the Gulf of Riga (region of Rukhnu Island) on the 23rd of November 1956, time of netting - 19.30 - 19.40.

Netting horizons in m	Under 1 m ²
0 - 5	430
5 - 10	200
10 - 20	80
20 - 23	133
0 - 23	843

The increased activity of the vertical migrations of Pontoporeia during the autumn-winter period makes it more accessible to pelagic fishes. In the Gulf of Riga the Baltic herring [Clupea harengus membras] changes over to feeding on Pontoporeia from November. Thus, in November 1956 80% of the Baltic herring in the benthopelagic concentrations, caught by trawling at the bottom, was feeding on Pontoporeia (mainly P. affinis).

According to the data of Jespersen (11), the herring in the region of Bornholm Island feed predominantly on mysids

and amphipods (P. femorata) during the autumn and winter. In the northern Baltic, especially in the Gulfs of Riga and Finland, these crustaceans are consumed in large numbers by the smelt [Osmerus eperlanus], as well as by the Baltic herring.

Characteristically, the mature males of Pontoporeia manifest an especially high migrational activity. This is strikingly evident by their pronounced predominance not only in the plankton samples but also in the stomachs of the Baltic herring and smelt. Segerstråle (1938) published a special study on this subject: "The mature males of Pontoporeia affinis as seasonal food of the smelt". In the stomachs of the 82 smelt that he studied (prevailing length of fish 15-19 cm), collected in November 1931 and 1936 in the Gulf of Finland, there were found about 200 specimens* of this crustacean, i.e. on average 25 crustaceans in one stomach, and mature males comprised from 90 to 97% of these¹.

VERTICAL MIGRATIONS OF COPEPODS

Daily vertical migrations have been established for all of the species, that occur in massive numbers, of the planktonic crustaceans in the Baltic: Pseudocalanus elongatus, Limnocalanus grimaldii, Temora longicornis, Eurytemora hirundoides, Acartia bifilosa, A. longiremis and Centropages hamatus.

The amplitude of the migration of Pseudocalanus elongatus in the Baltic comprises no less than 100 m, though the different age stages of this crustacean migrate in different layers. Thus, for example, in the southern Baltic in May 1957

¹ In the stomachs of three fish there were 125, 135 and 152 crustaceans.

* Sic. Should be "about 2000 specimens". (Tr.).

in the middle of the night, the maximal numbers of individual of copepodid stages I and II were found in the 0-10 m layer; of stage III - in the 10-25 m layer; of stages IV and V - in the 25-50 m layer, and of stage VI - in the 50-100 (106) m layer. In the middle of the day copepodid stages I and II of Pseudocalanus were concentrated in the 25-50 m layer, while all the rest were in the 50-100 m layer. Consequently, the main part of the Pseudocalanus population of copepodid stages I and II migrated at depths of from 0 to 50 m; of stage III - from 10 to 100-50 m; of stages IV and V - from 25 to 100-50 m, and of stage VI - within the 100-50 m layer.

Limnocalanus grimaldii performs daily migrations throughout the course of the whole year. In this species, as in Pseudocalanus, the migration limits depend on the age. According to the data of N. S. Khromov, in the Gulf of Riga in July at a station with a depth of 31 m the main part of the population of stages II-IV migrated within the limits of from 10 to 25 m, individuals of stage V moved from 10 to 30 m, while those of stage VI moved within limits of from 20 to 30 m.

In August 1957 Limnocalanus (developmental stages V-VI) migrated within the limits of the entire water column in the Gulf of Riga (0-50 m), though the bulk of the population (more than 80%) accomplished the migrations only within the depth limits of 30-40 (50) m. A more detailed representation of the migrations of the adult (stage VI) Limnocalanus in the Gulf of Riga in August may be obtained by considering its vertical distribution at the day station of August 14-15, 1957, that was obtained in calm and almost cloudless weather (Table 9).

Table 9

Таблица 9

A Горизонты лова в м	B Время наблюдений в час. и мин.									
	15.00-15.30		20.00-20.30		24.00-0.30		3.00-3.30		12.00-12.30	
	абсолют- ная чис- ленность	%	абсолют- ная чис- ленность	%	абсолют- ная чис- ленность	%	абсолют- ная чис- ленность	%	абсолют- ная чис- ленность	%
0-5	0	0	0	0	58	1,8	14	0,3	0	0
5-10	0	0	2	0,05	52	1,6	56	0,9	0	0
10-15	0	0	50	1,0	220	6,8	96	1,5	0	0
15-20	0	0	72	1,2	110	3,4	54	0,8	0	0
20-25	0	0	138	2,3	120	3,7	70	1,1	0	0
25-30	2	0,1	616	10,3	258	8,0	560	8,8	14	0,4
30-35	1164	39,9	1608	2,8	656	20,4	3246	51,6	66	1,8
35-40	1740	60,0	3460	58,4	1748	54,3	2192	35,0	3550	97,8

A - Netting horizons in m

B - Times of observation in hours and minutes

c - absolute numbers

In the middle of the day (12.00-12.30 according to the table) 97.8% of the entire population of Limnocalanus was found in the benthopelagic 5-meter layer (40-35 m), while in the middle of the night only 54.3% remained here. Thus, 43.4% of the Limnocalanus population performed a vertical migration in the 24-hour period under consideration. A considerable part of the population (20.4%) migrated only from the 35-40 m layer to the 30-35 m layer. 17.2% of the population migrated higher than 15 m from the bottom, 10.2% - higher than 25 m, and 3.4% - higher than 30 m; 1.8% of the population was in the uppermost 5-meter layer of the water.

The ascent, in the middle of the night, of approximately 10% of the Limnocalanus population into the 1-15 m layer, where the water temperature is 16.6-17.6° (Figure 4), is an example of the gradual adaptation of this Arctic species to



Figure 4. The vertical distribution of Limnocalanus in the Gulf of Riga on August 14 - 15, 1957.

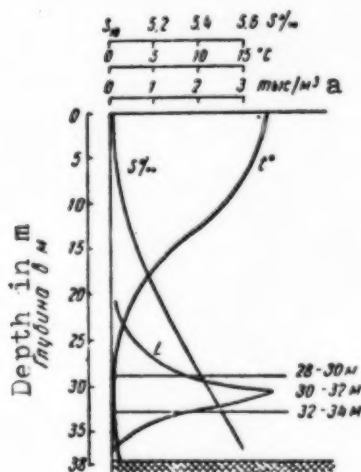


Figure 5.

The vertical distribution of Limnocalanus in the Gulf of Riga on July 14, 1957, in the middle of the day at station 134.

a - thou./m³

the conditions of the elevated temperature of the Baltic waters, in particular of the Gulf of Riga, in the summer in the upper 0-15 (20)-meter layer of the water. The ascent of Limnocalanus into the warm layers of water is undoubtedly associated with the search for the most concentrated food (microplankton).

For a more detailed determination of the stratification of Limnocalanus, a series was taken in July 1957 at one of the central stations in the Gulf of Riga, with netting of the column of water every 2 meters. It was found (Figure 5) that in the middle of the day the greatest concentration of Limnocalanus was not right at the bottom but rather 6-8 m higher, i.e. in the layer from 30 to 32 m at a total depth of 38.5 m at this station. Microstratification (clearly expressed differences in the numbers within 2-4 m limits along the vertical) is observed with Limnocalanus. Thus, for example, the Limnocalanus numbered 3800 individuals per 1 m^3 in the 30-32 m layer; 2 m deeper (32-34 m) there were 1505 individuals or 39% of its numbers in the 30-32 m layer, while in the layer 2 m higher (28-30 m) there were 1530 individuals per 1 m^3 or 40% of the numbers in the highest density layer.

The causes of the microstratification of Limnocalanus have not been elucidated. The vertical trend in the temperature and salinity in the microstratification zone has an extremely small gradient (see Figure 5). Apparently these factors do not influence the microstratification of Limnocalanus. It is more probable that the cause of this is the uneven illuminance of the water or a change in the gaseous regime, which is not infrequently found in the benthopelagic layers of bodies of water.

The macrodistribution of Limnocalanus in the Gulf of Riga during the summer has two characteristic features.

1. At all depths the main part of the population (more than 60%) is concentrated in the 10-meter layer of water next to the bottom.

Table 10

Таблица 10

А Средняя глубина на станциях в м	В Число станций	С Количество <u>Limnocalanus</u> под 1 м ² поверхности воды	Д Биомасса в г под 1 м ² поверхности воды
0-9	4	0	0
10-19	8	0	0
20-29	10	100	0,035
30-39	7	4 600	1,61
40-49	6	19 840	6,94
50-53	2	30 700	10,75

A - Average depth at stations in m

B - Number of stations

C -- Number of Limnocalanus under 1 m² water surface

D - Biomass in g under 1 m² water surface

2. Limnocalanus is absent or is very rarely encountered (several tens per 1 m³) at depths of less than 25 m; at depths of more than 30 m its numbers increase rapidly as the depth increases (see Table 11).

The average numbers and biomass of Limnocalanus in the Gulf of Riga in August 1957 are presented in Table 10.

These features of the distribution of Limnocalanus, the largest and nutritionally most valuable representative of the zooplankton, may be explained only by its being consumed more intensely by fishes. In the Gulf of Riga at medium depths, where the conditions are favourable for the normal development of Limnocalanus (with the good food supply, there should be more of it here than in the zone of the greatest depths), it is fed upon severely during the daytime in summer by the Baltic herring, sprat [Clupea sprattus balticus], smelt and other fishes. Limnocalanus does not reproduce throughout the entire

Table 11

Таблица 11						
А Горизонты лова в м	26/V 1956	15/VIII 1957	21/IX 1957	26/V 1956	15/VIII 1957	21/IX 1957
	13 час. 30 мин. 13.30	12 час. 12.00	17 час. 17.00	23 час. — 23 час. 30 мин. 23.00 —	24 час. — 0 час. 30 мин. 24.00 —	21 час. — 21 час. 30 мин. 21.00 —
0—10	7	0	4	23.30	24.30	21.30
10—20	16	0	11	21	3	50
20—30	21	2	37	24	10	44
30—40	56	98	48	44	12	6
				11	75	0
	100	100	100	100	100	100

A - Netting horizons in m

summer and autumn, and therefore the changes in its population from April - May proceed in two directions: an increase in the numbers (initially of the absolute numbers, and then from July - August only of the relative numbers) of the older age groups and an overall reduction in the population numbers as a consequence of the natural mortality and their being fed on by the fishes. As a result, by August only a small part of the population survives at a depth of more than 30 m, which towards the end of this month is composed of 95-98% adult individuals and 2 - 5% of individuals of copepodid stage V.

For characterizing the intensity of the seasonal migrations of Limnocalanus data are presented in Table 11 on its vertical distribution in the Gulf of Riga (as %) in the spring, summer and autumn, during the night and during the day.

The most intensive migrations in Limnocalanus were observed in the autumn; in the summer they are weakly expressed. The difference in the quantitative composition of the population in the benthopelagic layer during the day and during the

night, expressed in percentages, serves as an index of the intensity of migration. This index may also be expressed in the form of a coefficient. Thus, at the end of May the intensity of migration for the 30-40 m layer was determined as 45% of the total population, which is equivalent to a 0.45 coefficient; in the middle of August the migration intensity was half as great - 23% (0.23 coefficient), while in November* (from 17.00 to 21.00) in the benthopelagic layer 48% (0.48 coefficient) migrated.

The intensification of the vertical migrations of Limnocalanus in the autumn, as compared with the migrations in the summer and even in the spring, is explained by the absence of a vertical temperature stratification at this time (from the end of October) in the Gulf of Riga.

The total range of the migrations of Temora longicornis is as much as 100-120 m, though the major part of the population migrates only within limits of 30-40 m in the course of a 24 hour period. During the spring in the central Baltic the main part of the population of Temora keeps to depths of from 10 to 25 m during the day, while at night 95% of the population is concentrated in the uppermost layer from 0 to 10 m. During the day about one fifth of the population (19.5%) is located in the layer from 50 to 106 m, while only 2% is found there in the middle of the night. Predominantly adult individuals of copepodid stages VI and in part V migrate to a depth of more than 50 m.

During the summer the migrations of Temora in the layer from 0 to 50 m are expressed as clearly as in the spring.

* Sic. In Table 11, however, indicated as September (IX). (Tr.).

Table 12

Таблица 12

А Горизонты лова в м	В Время наблюдений в час. и мин.							
	20.00-20.20		0 40-0.50		12.40-12.50		16.40-16.50	
	С числен- ность в 1 м ³	в % in %	С числен- ность в 1 м ³	в %	С числен- ность в 1 м ³	в %	С числен- ность в 1 м ³	в %
0-10	5160	89,0	11620	92,4	100	1,8	70	2,8
10-50	620	10,7	1020	7,6	5200	97,9	2410	95,2
50-75	20	0,3	0	0	10	0,3	50	2,0

A - Netting horizons in m

B - Times of observation in hours and minutes

c - numbers in 1 m³

In Table 12 are presented data on the vertical distribution of Temora longicornis in the central Baltic on July 15-16, 1949.

Eurytemora hirundoides migrates mainly in the 20-30-meter layer of water. In the Gulf of Riga in May and August 96-98% of the total number of individuals of the population of this species (all of the copepodid stages) are concentrated in the uppermost layer of the water (0-10 m) in the middle of the night, while in the middle of the day from 34% (in May) to 50% (in August) descend to a depth of from 10 to 30 m. During daytime in August two peaks in the numbers were noted in the vertical distribution of Eurytemora in the Gulf of Riga: one in the 0-10 m layer (with a maximum in the 5-10 m layer) and the second in the 20-30 m layer (with a maximum in the 25-30 m layer in the middle of the day, and in the 20-25 m layer at about 15.00), and moreover the concentration in the 20-30 m layer at some hours of the day is considerably greater than the concentration in the upper 10-meter layer.

Table 13

А Горизонты лова в м	Время наблюдений в час. и мин.					
	20.00—21.30		23.00—23.30		13.00—13.30	
	численность в 1 м ³	в % in %	численность в 1 м ³	в %	численность в 1 м ³	в %
0—10	5600	93	5300	96	4900	64
10—20	130	2	50	1	2550	34
20—30	300	5	0	0	100	1
30—40	0	0	190	3	100	1

А - Netting horizons in m

В - Times of observation in hours and minutes

с - numbers in 1 m³

Data on the vertical distribution of Eurytemora (all copepodid stages) in the Gulf of Riga on May 26 - 27, 1956, are presented in Table 13.

According to the data of Bogorov (1), in the Caspian Sea Eurytemora (another species - E. grimmi) migrates more intensively than in the Baltic, and its migrations extend to a depth of 83 m.

The vertical migrations of Acartia, in both the central part of the Baltic Sea as well as in the Gulf of Riga, are expressed only within the limits of 25 - 40 m and are not as distinctly expressed as in the other copepods considered above. In this species one sometimes observes during the summer a clearly expressed two-layered stratification. Thus, for example, on August 13 - 14, 1957, in the Gulf of Riga the largest accumulations of Acartia were in the 0 - 5 m layer and the 10 - 15 m layer in the middle of the night, while in the middle of the day the highest concentrations were found in the 5 - 10 m and 15 - 20 m layers.

According to the data of Hentschel (14), in the Fehmarn Belt this species accomplishes distinct migrations within the upper 10 m: the maximal numbers of sexually mature individuals are found during the day at a depth of 10 m, while at night they are at a depth of 5 m.

CONCLUSION

In connection with the vertical migrations of the copepod species that occur in massive numbers in the Baltic Sea, large daily changes are found in the food value of the different layers of water (the biomass of the food plankton located in these layers). The dimension of these changes may be evaluated on the basis of the following data. In the Gulf of Riga in August 1957 during the day (from 05.00 to 19.00) 40% of the biomass of the planktonic crustaceans was concentrated in the 19-meter benthopelagic layer of water (from 30 to 40 m) and only 20% was found in the uppermost layer (from 0 to 10 m).

In contrast, during the night 42% of the total biomass was in the upper 10-meter layer, while 19% was in the benthopelagic layer. These changes were expressed even more clearly in the southern Baltic in May 1957. Thus, at a 24-hour station in the Gdansk basin, the biomass of the food plankton in the upper 10-meter layer from 00.00 to 04.00 comprised 63-70% of the biomass of the entire water column (0-106 m), while in the layer from 50 to 106 m there was only 1-5% of the biomass; during the day (at 12.00 to 12.30) 7% of the total biomass was in the upper layer, while 48% was in the 50-106 m layer. Consequently, the changes in the comparative size of the biomass during the course of a day in the 0-10 m layer attain a

ratio of 1 : 10, while in the 50-106 m layer this ratio is 1 : 48.

These differences in the food value of the different layers of water during the course of a day will be expressed even more clearly if the biomass of the migrating mysids and amphipods is added to the biomass of the food plankton.

Besides crustaceans, distinct vertical migrations during the course of a day are also accomplished by the larvae and young of fishes, as well as by adult fishes, including the Baltic herring, sprat and cod, which is well known in fisheries practice in the Baltic.

The daily vertical migrations of the planktonic and benthoplanktonic crustaceans in the Baltic are most clearly expressed in those species of copepods, mysids and amphipods which are present in the greatest numbers, i.e. in that complex which in aggregate comprises the basis of the food of all of the main commercial fishes: the sprat (copepods and mysids), the Baltic herring (copepods, mysids and amphipods), the smelt (mysids, amphipods and copepods), the flounder (amphipods and mysids), as well as young and, in part, mature cod (mysids and amphipods), young whitefish (amphipods), etc. This provides yet another piece of evidence for the protective-adaptive significance of vertical migrations in invertebrates, to the consideration of which special studies by the author have been devoted (5, 6). This point of view was first put forward by M. M. Kozhov (4).

One should also mention facts that seemingly restrict a particular thesis or even contradict this. This concerns crustaceans which play an important role in the feeding of

fishes but do not perform vertical migrations. In the Baltic Bosmina coregoni maritima, which displays a very strong development from July to September, is one such crustacean.

In some years in the central basin of the sea, as well as in the Gulfs of Riga and Finland, in August - September Bosmina comprises the main food of the sprat and young Baltic herring. This species sometimes attains huge numbers (up to 70 thousand individuals per 1 m³) in the uppermost layer, but it does not perform daily migrations.

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